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Early origin of viviparity in the mammalian lineage

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Viviparity is a reproductive mode in which the embryo completes their development inside the female body. Present-day mammals, with the exception of monotremes, are viviparous, as opposed to the egg-laying reproductive mode of most vertebrates. Non-therian cynodonts are regarded as oviparous although direct evidence on the reproductive modes in extinct taxa is lacking. We identified, in a palaeohistological study, a neonatal line in two bones of the early probainognathian *Chiniquodon theotonicus* from the Late Triassic of South America. The body mass at birth is comparable to that observed in living placentals, and notably higher than the one registered for monotremes, marsupials, lepidosaurs, crocodiles, and birds. Our results reveal that viviparity is not exclusive of therians among synapsids, pushing back its recognition in the clade ~90–95Myr.

KEYWORDS
Cynodontia, evolution, paleohistology, Triassic, viviparity

1 Introduction

Viviparity is an important acquisition in mammalian evolution, characteristic of modern therians and thought to have played a key role in their evolutionary success (Blackburn, 1999). This reproductive mode contrasts with oviparity, the plesiomorphic condition for vertebrates (Packard et al., 1977; Angelini and Ghiara, 1984; Rothchild, 2003). Nevertheless, viviparity has evolved independently more than 150 times among vertebrates (Packard et al., 1977; Blackburn, 2015). Extant therians share a complex array of coadapted features (such as placentation, lactation, and its endocrine regulation) that suggest that viviparity is a synapomorphy of the clade (Angelini and Ghiara, 1984; Guillette and Hotton, 1986; Lillegraven et al., 1987; Tyndale-Biscoe and Renfree, 1987; Packard et al., 1989; but see Sharman, 1970, 1976; Packard et al., 1977). Monotremes, despite presenting some sort of placentation (i.e., absorption of oviductal secretions as opposed to the yolk sac or chorioallantoic types of placenta present in therians), lay eggs (Blackburn, 2015).

Non-mammalian synapsids have been regarded as oviparous (Guillette and Hotton, 1986; Lillegraven et al., 1987), although no fossil eggs assignable to them were found. Only recently, the finding of an embryo of the dicynodont *Lystrosaurus* in an *in ovo* position demonstrated oviparity in early synapsids (Benoit et al., 2026). Despite being unknown, it

has been generally upheld that early synapsid eggs were soft-shelled, and thus, unlikely to fossilize (Hill, 1933; Sander, 2012; Hoffman and Rowe, 2018). There is an abundant synapsid fossil record from several Palaeozoic and Mesozoic localities, including lagerstätten and mass-mortality deposits (e.g., Wang et al., 1998; Kielan-Jaworowska et al., 2004; Kemp, 2005; Fürsich et al., 2007; Jiang et al., 2014; Mancuso et al., 2014; Meng, 2014; Zhou, 2014). Furthermore, some early cynodonts have been proposed to live in intraspecific aggregations (Jasinoski and Abdala, 2017) and to have inhabited burrows (Smith, 1987; Damiani et al., 2003; Abdala et al., 2006; Fernandez et al., 2013), scenarios that are expected to enhance the preservation potential of eggs and/or perinatal individuals. Nevertheless, there is a single record of perinatal non-mammalian cynodonts (Hoffman and Rowe, 2018), but it is inconclusive regarding if a viviparous or oviparous reproductive mode was in place.

Previous attempts to discern if non-mammalian cynodonts laid eggs or gave birth to fully developed offspring have failed because evidence from extant amniotes is insufficient to properly test such hypotheses (Lillegraven, 1979; Renfree et al., 2009). Current theories assume a single evolutionary origin of viviparity in the synapsid lineage, at the base of Theria (Lillegraven, 1979; Guillette and Hotton, 1986; Lillegraven et al., 1987; Tyndale-Biscoe and Renfree, 1987; Packard et al., 1989; Guillette, 1991; Renfree et al., 2009; Blackburn, 2015). Here we challenge the universally accepted hypothesis that all non-therian cynodonts were oviparous (Ferner et al., 2017*)* and reveal that viviparity evolved in the synapsid clade as early as the early Late Triassic (~236 Myr) among non-mammaliaform cynodonts, predating the estimated origin of Theria in the Late Jurassic-Early Cretaceous (Bininda-Emonds et al., 2007; Luo, 2007*)*.

2 Results

We report on new information supplied by *Chiniquodon theotonicus* specimen CRILAR-PV109 (Figure 1A), which was found in the traditional, rich fossiliferous levels of the Chañares Formation (Carnian, early Late Triassic) in north-western Argentina (Mancuso et al., 2014; Marsicano et al., 2016). It is a partially articulated skeleton, including skull and several postcranial elements. There are more than 50 *Chiniquodon theotonicus* specimens recovered from the Chañares Formation, ranging in skull length from ~50 mm to about ~160 mm. With a basal skull length of 160 mm, CRILAR-PV109 is among the largest individuals reported for this species in the unit (Abdala and Giannini, 2002; Mancuso et al., 2014). Hence, considering the relatively high number of known specimens of *Chiniquodon theotonicus* and their size range, we argue that the studied *Chiniquodon theotonicus* specimen (CRILAR-PV109) is large enough to be interpreted as an adult, and most probably a fully grown animal. This working hypothesis is also supported by the fact that all skull bones are strongly sutured to each other, all teeth are fully erupted, and the postcranium is completely ossified, including tarsal and carpal bones.

2.1 Paleohistology

The femoral and ulnar cortices in *Chiniquodon theotonicus* specimen CRILAR-PV109 are almost entirely formed of densely vascularized fibrolamellar bone tissue, which is a composite primary tissue formed by a periosteal matrix of woven fibered bone with a lamellar bone matrix of intracortical origin lining the vascular spaces (primary osteons) (Figures 1B–H; Supplementary Figures S1–S4; see Supplementary Material for detailed histological descriptions). Vascularization mostly consists of abundant radially oriented canals (longitudinal and circumferential canals are also present, but in a minor density) (Figures 1B–H; Supplementary Figures S3, S4).

The examined long bones of *Chiniquodon theotonicus* show medullary cavities of exceptionally small diameter, which, in combination with the little secondary remodeling, resulted in the preservation of embryonic tissues. An abrupt change in the histological pattern of *Chiniquodon theotonicus* specimen CRILAR-PV109 is observed in the innermost preserved primary bone tissue, which contains a minor density of mostly longitudinally oriented vascular canals (Figures 1E, F; Supplementary Figures S1–S4). The internal diameter of the vascular canals in the perimedullary region is also noticeably reduced in comparison to that observed in most of the cortex. In addition, the matrix of the fibrolamellar bone exhibits a higher amount of concentrically arranged fibers (Figures 1E, F; Supplementary Figures S1–S4), being the modification in the intrinsic fiber arrangement more pronounced in the ulna (Supplementary Figures S1, S3). The abrupt histological change between the perimedullary and the more external region in the femur and ulna of the *Chiniquodon theotonicus* specimen studied here represents an event that occurred very early in the life history of this animal and can be interpreted as a growth mark related to birth (i.e., neonatal line; see Discussion).

2.2 Body-mass estimations and comparisons with extant amniotes

The neonatal line represents the bone circumference at the moment of birth (Nacarino-Meneses and Köhler, 2018), which can be employed for body-mass estimations (Anderson et al., 1985; Anyonge, 1993), a proxy to body size. Hence, we used different regression equations to estimate the body mass reached by this individual and compared the results to the weight at the time of birth, as marked by the neonatal line. Body-mass estimations for *Chiniquodon theotonicus* were based on the femoral circumference at mid-shaft, using three equations originally proposed for carnivorans (in general) and specifically for felids and for canids *(*Anyonge, 1993*)*. All three methods predict an almost identical body mass for *Chiniquodon theotonicus* at the moment of death (Supplementary Table S1). The regressions based on all carnivoran species and on felids resulted in very similar estimations for the neonate body mass whereas the canid equation resulted in a proportionally high value (almost double). This suggests that the canids-based equation might not be useful for very small individuals and should be considered with care. The body-mass averages

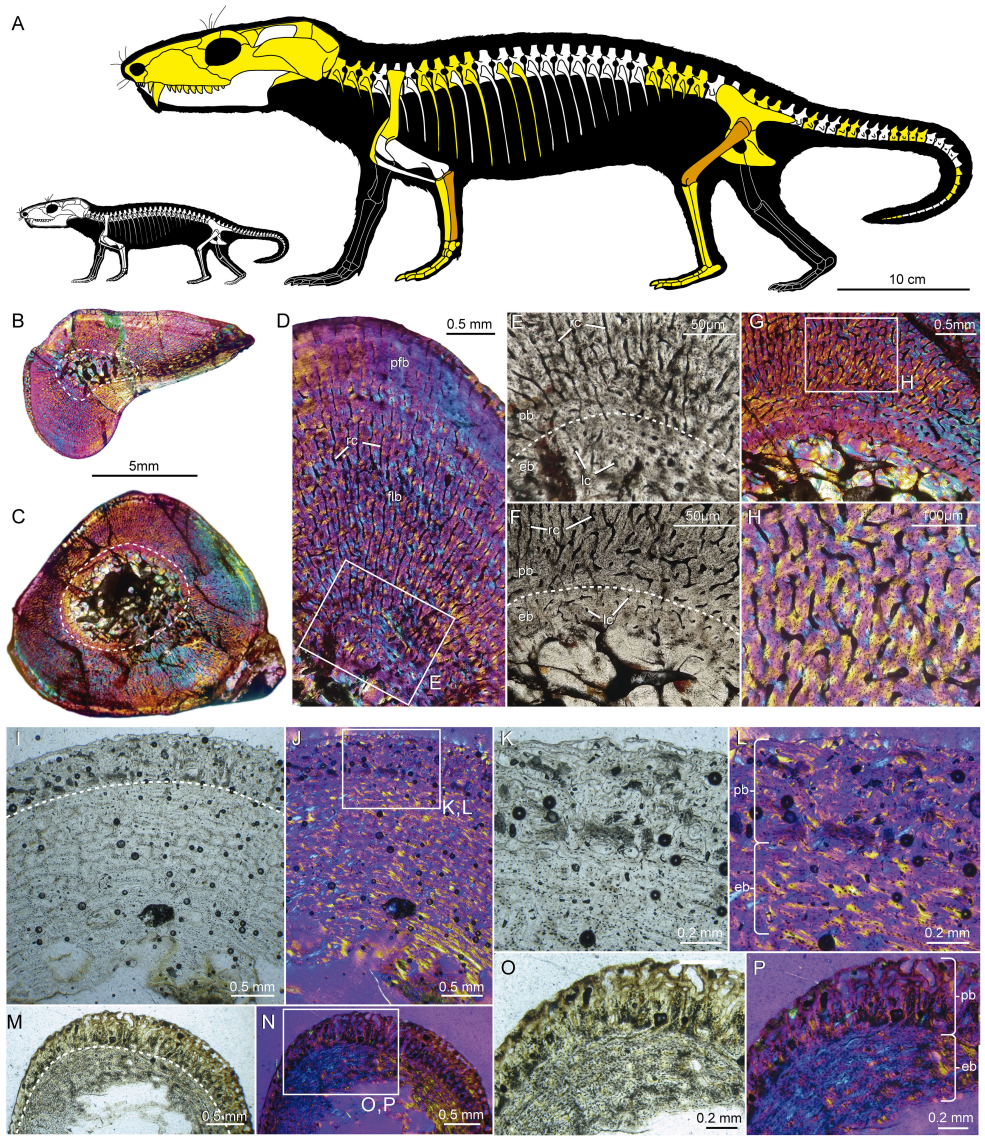

FIGURE 1
Palaeohistology of *Chiniquodon theotonicus* and examples of neonatal lines in extant placental mammals. **(A)** Representation of neonate and adult *Chiniquodon theotonicus*. Recovered (yellow) and histologically analyzed (orange) bones of specimen CRILAR-PV109. Skeleton outline modified from Romer and Lewis (1973). Cross section of the ulna **(B)** and the femur **(C)**. **(D)** Cortical bone of the ulna mostly formed by fibrolamellar bone (flb) tissue with abundant radially oriented vascular canals (rc). Parallel fibered bone (pfb) in the outer cortex indicates a reduction in the growth rate. **(E)** Transition between embryonic (eb) and postnatal bone (pb) tissue in the inner cortex of the ulna. Embryonic tissue is less vascularized and exhibits predominance of longitudinally oriented vascular canals (lc). **(F, G)** general view **(F)** and detail **(G)** of the inner cortex of the femur showing the transition between embryonic and postnatal bone tissue. **(H)** Highly vascularized fibrolamellar bone tissue formed in the femur. **(I–P)** Histological sections of the humerus in *Sus scrofa* **(I–L)** and *Lagostomus maximus* **(M–P)**. General view **(I, J, M, N)** and detail **(K, L, O,P)** of the transition between the embryonic and the postnatal bone. Dashed line signals the position of the neonatal line.

resultant from using Anyonge's (1993) equations are 11.99 kg at the time of death and 1.68 kg for the neonate, representing the body mass at birth 14.04% of the maximum weight reached.

With the aim to test our results regarding the body mass of *Chiniquodon theotonicus* at the time of death, we used the skull length as a proxy to body weight. We employed an equation based on data from extant carnivorans (van Valkenburgh, 1990; Mancuso et al., 2014). Furthermore, considering our estimations of the *Chiniquodon theotonicus* neonate body mass and utilizing the same equation (van Valkenburgh, 1990), we calculated the approximate length of the skull at the moment of birth on the basis of the estimated body weight from the neonatal line. We found that the estimations using the skull length are congruent with those calculated from the femoral circumference employing equations based on all carnivoran, felid, and canid species. In addition, it is predicted that the skull length of the *Chiniquodon theotonicus* (CRILAR-PV109) neonate would have been between 40 mm and 50 mm. This length range is similar to that of the smallest *Chiniquodon theotonicus* skulls known, i.e., specimens MCZ 4296 and PVL 4675 (Abdala and Giannini, 2002). Hence, we propose that these latter specimens represent perinates, a suggestion that is also supported by the recognition of several features suggestive of a very young age (e.g., number of teeth, skull proportions, bone morphology).

To test the hypothesis that *Chiniquodon theotonicus* reproductive strategy was more similar to that of placental mammals than to

other amniotes, we compared the estimated body mass of specimen CRILAR-PV109 at the time of birth and death with hatchling, neonate, and adult body masses of extant amniotes, including 1869 mammals, 2619 non-avian reptiles, and 782 birds (Supplementary Data S1-S3). The neonate body mass predicted for *Chiniquodon theotonicus* is most comparable to that observed in extant placentals of similar adult sizes (Figure 2). The neonate to maximum-reached body weight proportion estimated for *Chiniquodon theotonicus* (i.e., between 10% and 20%) is similar to placentals of a broad phylogenetic spectrum (Figure 2A; Supplementary Data S1). On the contrary, monotremes and marsupials are extremely small at birth, most of them less than 0.15% of the adult body mass

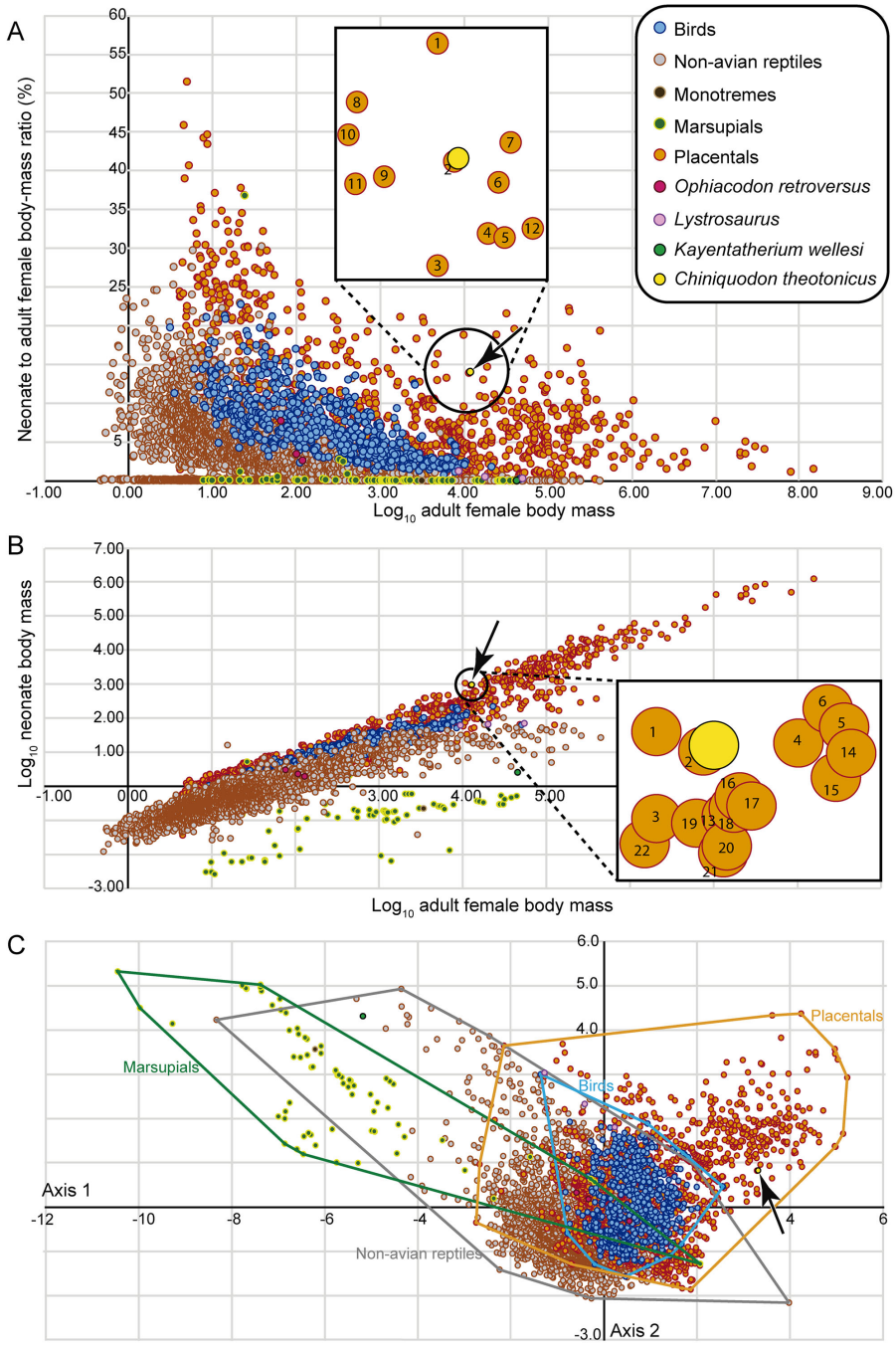

FIGURE 2
Neonate and adult mass of *Chiniquodon theotonicus* and other amniotes. **(A)** Neonate to adult body-mass ratio (%) plotted against the decimal logarithm of the adult female body mass, with magnified circled area. **(B)** Log_{10}-log_{10} plot of the neonate body mass versus the adult mass, with magnified circled area. **(C)** Discriminant analysis showing convex hulls for data from extant non-avian reptiles, birds, marsupials, and placentals. The average of the estimations from *Chiniquodon theotonicus* are represented (arrow). Data and sources can be found in Myhrvold et al. (2015). Abbreviations: 1, *Cephalophus adersi*; 2, *Cephalophus dorsalis*; 3, *Cephalophus natalensis*; 4, *Cephalophus zebra*; 5, *Cephalophus niger*; 6, *Ourebia ourebi*; 7, *Cephalophus callipygus*; 8, *Philantomba monticola*; 9, *Philantomba maxwellii*; 10, *Madoqua guentheri*; 11, *Madoqua kirkii*; 12, *Eudorcas thomsonii*; 13, *Cephalophus rufilatus*; 14, *Sylvicapra grimmia*; 15, *Muntiacus muntjak*; 16, *Oreotragus oreotragus*; 17, *Muntiacus reevesi* and *Muntiacus rooseveltorum*; 18, *Hydropotes inermis*; 19, *Raphicerus campestris*; 20, *Dinomys branickii*; 21, *Moschus chrysogaster*; 22, *Pudu puda*.

(Grant, 2007; Renfree et al., 2009) (Figure 2B; Supplementary Data S1). Lepidosaurs, crocodiles, birds, and placentals share a comparable tendency in which larger adults produce larger younglings, and a similar range of variation of the neonate to adult body-mass proportion (Figure 2B; Supplementary Data S1–S3). However, independently of their reproductive mode, adult lepidosaurs and crocodiles of more than 10 kg produce relatively small offspring when compared to placental mammals (Figure 2B; Supplementary Data S1, S2). In these taxa, the hatchlings do not represent more than 0.62% of the female body weight. Extant birds with adult body weights above 10 kg, produce hatchlings heavier than those of lepidosaurs and crocodiles and comparable to some placentals (Figure 2B; Supplementary Data S1, S3). Nevertheless, in these bird species, the hatchling weight represents a relatively small percentage of the adult body mass (between 0.002% and 0.024%). Conversely, similar sized placentals can give birth to notably larger younglings that can represent more than 22% of the adult body mass.

In order to statistically test the observation that estimations of the body mass of *Chiniquodon theotonicus* are in line with data from placental mammals (Figures 2A, B), we performed a discriminant analysis and a K-nearest neighbors test (Supplementary Data S4). We used the log transformed neonate and adult body-mass estimates for *Chiniquodon theotonicus* to infer to which extant amniote clade it is more similar (Figure 2C). In every case, *Chiniquodon theotonicus* was grouped with placentals with high probability.

Evidence regarding reproductive strategies in non-mammalian synapsids has also been presented for the early form *Ophiacodon retroversus*, the dicynodont *Lystrosaurus*, and the non-mammaliaform cynodont *Kayentatherium wellesi* (Shelton and Sander, 2017; Hoffman and Rowe, 2018; Benoit et al., 2026). Accordingly, we included these taxa in our database in order to analyze how they compare to extant amniotes.

Including *Ophiacodon retroversus* in our study is methodologically prevented by the fact that the equations employed in our manuscript require the femoral circumference, a datum that it is not available for the hatchling/neonate specimen reported for this taxon (Shelton and Sander, 2017). However, the humeral circumference could be employed instead of the femoral one, considering that the circumference of these two bones is similar (see Methods). The perinate to adult body-mass ratio in *Ophiacodon retroversus* (between 2.62% and 7.76%, depending on the equation used for estimating the body mass) is like that of some placentals, non-avian reptiles, and birds, whereas it is much higher than that of marsupials or monotremes with equivalent weight as adults (Figure 2A). Conversely, the body mass of the hatchlings of *Ophiacodon retroversus* is found to be comparable to that of some non-avian reptiles, and much lower than that of placentals and birds of similar adult sizes (Figure 2B). The K-nearest neighbors analysis classifies it alternatively as a non-avian reptile, a bird or a placental (Supplementary Data S4).

In the case of *Lystrosaurus*, we considered the body-mass estimations for the adult (i.e., 8.825 kg, 18.511 kg, and 50 kg) and the perinate (i.e., 115 g) as proposed in the literature (Benoit et al., 2026 and references therein). The perinate to adult body-mass ratio in *Lystrosaurus* (between 0.2% and 1.3% depending on the adult body mass considered) is most similar to that of some birds, whereas it is lower than that of placentals and higher than that of non-avian reptiles, marsupials or monotremes with equivalent weight as adults (Figure 2A). The body mass of the hatchlings of *Lystrosaurus* is lower than that of most placentals and birds, and larger than that of most non-avian reptiles of similar adult sizes (Figure 2B). When included in the discriminant analysis (Supplementary Data S4), *Lystrosaurus* is plotted in the intersection between the non-avian reptile, the avian, and the placental fields (Figure 2C). In addition, the K-nearest neighbors analysis shows that it is classified alternatively as a non-avian reptile, a bird or a placental.

Regarding the tritylodontid *Kayentatherium wellesi*, we found that the perinate to adult body-mass ratio in *Kayentatherium wellesi* (0.01%) is most similar to that of monotremes, marsupials, and non-avian reptiles, and lower than that of birds and placentals with equivalent weight as adults (Figure 2A). The proposed body mass of the perinates (i.e., 4.7 g; Hoffman and Rowe, 2018) is lower than that of non-avian reptiles, birds or placentals and larger than that of marsupials of similar adult sizes (Figure 2B). *Kayentatherium wellesi* was invariably classified as a non-avian reptile in the K-nearest neighbors analysis (Supplementary Data S4).

3 Discussion

The important histological change recognized between the perimedullary and the more external region in the femur and ulna of *Chiniquodon theotonicus* is coincident in timing and characteristics with a growth mark related to birth as observed in extant amniotes (Nacarino-Meneses and Köhler, 2018; Garrone et al., 2019; Figure 1I–P). The presence of this non-cyclical growth mark is independent of the growth rate and has been reported in reptiles and mammals (e.g., Castanet and Baez, 1991; Nacarino-Meneses and Köhler, 2018; Garrone et al., 2019). Whether this mark is a neonatal or a hatching line cannot be distinguished histologically, but evidence supporting one or the other reproductive mode (i.e., viviparous or oviparous) is available through body-mass comparisons.

Data from extant amniotes, as presented herein, strongly support that the structure recognized in *Chiniquodon theotonicus* is a neonatal line (e.g., Castanet and Baez, 1991; Nacarino-Meneses and Köhler, 2018; Prondvai et al., 2022). The neonatal line represents a quick change in the rate of bone deposition, with an acceleration in growth rate after the event of birth (Nacarino-Meneses and Köhler, 2018). This shift in the rate of bone deposition is not necessarily represented by a line of arrested growth (LAG; Garrone et al., 2019; Calderon et al., 2021) and has been related to changes in bone tissue type, including variations in the fibrillar organization (i.e., from a more organized to a more disorganized bone matrix) and in the arrangement and size of the vascular canals (i.e., from smaller, mainly longitudinal canals to larger, mostly radial canals) in extant placentals (Nacarino-Meneses and Köhler, 2018; Garrone et al., 2019; Calderon et al., 2021). It is noteworthy

that the histological features related to the neonatal line differ among living placentals (e.g., different species of extant horses, the large rodent *Lagostomus maximus*, and *Sus scrofa*; Nacarino-Meneses and Köhler, 2018; Garrone et al., 2019; Figures 1I–P), even between bones of the same species (Nacarino-Meneses and Köhler, 2018). However, in every case, the histological features recognized are interpreted to represent an abrupt acceleration in the growth rate, such as in the femur and ulna of *Chiniquodon theotonicus*. The histological changes that follow the neonatal line have been related to an increase in the bone deposition rate and in the biomechanical requirements for weight-bearing and locomotion immediately after birth (Anderson et al., 1985; Nacarino-Meneses and Köhler, 2018; de Buffrénil et al., 2021a).

It is rare for neonatal lines and other similar histological structures (e.g., hatching line) to be preserved, except for very-young individuals, because the expansion of the medullary cavity occurs usually shortly after birth and causes the embryonic bone to be reabsorbed (Nacarino-Meneses and Köhler, 2018; Garrone et al., 2019). However, there are cases where remnants of embryonic tissue (including calcified cartilage) are preserved in the adult. Whereas this is common in aquatic-adapted forms such as sirenians, it can also occur in terrestrial forms (de Buffrénil et al., 2021b). Among non-mammalian synapsids, only the early form *Ophiacodon retroversus* has been reported to preserve embryonic tissues (Shelton and Sander, 2017). Embryonic tissues have not been previously recovered in any of the 25 studied species of non-mammalian cynodonts (de Ricqlès, 1969, 1972; Botha-Brink and Chinsamy, 2000, 2004; Botha, 2002; Ray et al., 2004; Botha and Chinsamy, 2005; Chinsamy and Hurum, 2006; Chinsamy and Abdala, 2008; Botha-Brink et al., 2012, 2018; Veiga et al., 2018; Butler et al., 2019; Garcia Marsà et al., 2022; Kulik, 2023).

Body-mass estimations of the studied specimen of *Chiniquodon theotonicus* (CRILAR-PV109) were obtained using equations constructed for the purpose of estimating the weight of extinct taxa. In particular, considering that our study required the body-mass estimation of a synapsid on the basis of measurements exclusively obtained from its femoral cross-section, we used equations presented by Anyonge (1993) based on extant mammals. Although we are aware that the modern species from which these equations were obtained could not be very appropriate analogues due to differences in body proportions or other biological traits (e.g., Wright et al., 2024; Kerber et al., 2025), these equations represent the best proxies available to our knowledge. Putative inaccuracies in the mass estimates at the time of birth and death of the *Chiniquodon theotonicus* specimen studied here are expected to be similarly biased, thus our inferences regarding the proportion between neonate and maximum-reached weight would remain valid. It has been suggested that equations based on adult individuals might not be accurate to estimate body mass at early ontogenetic stages due to the non-linear growth of mammals (Köhler, 2010). However, to the best of our knowledge, there are no published equations linking the femoral circumference and the body mass in non-biped mammals that have been constructed considering ontogeny. Hence, we have employed those equations available that have been accepted by the scientific community, following previous authors that encountered similar problems (e.g., Hoffman and Rowe, 2018).

Chiniquodon theotonicus inferred weight at birth and its neonate to maximum-reached body-mass proportion are larger than those of birds and most placentals of comparable adult sizes. The relatively high body-mass estimates obtained for *Chiniquodon theotonicus* around the time of birth are probably due to the equations retrieving larger body-mass predictions for very small individuals. Nevertheless, despite this issue, the body-mass estimations of the neonate *Chiniquodon theotonicus* are more comparable to that of extant placentals than to any other living amniote. The scarcely known postcranial skeleton of *Chiniquodon theotonicus* (e.g., Mocke et al., 2019) precludes the analysis of its pelvic anatomy, which could be a source of additional comparisons with extant placentals that give birth to relatively large younglings. Our results provide evidence of viviparity in *Chiniquodon theotonicus*, which ties in with recent findings showing that other remarkable features of present-day mammals (e.g., motile rhinarium, maxillary vibrissae, enlarged cerebellum, body hair coverage, and lactation) originated at the root of Probainognathia (Benoit et al., 2016; 2020) (Figure 3).

Our finding contrasts with the generally accepted idea that non-therian synapsids were oviparous, an hypothesis that is mostly untested. Evidence from early synapsids is available from *Ophiacodon retroversus*. The non-cyclical growth mark reported in a humerus of this taxon was interpreted as a hatching line, although the possibility of it being a neonatal line was not discussed (Shelton and Sander, 2017). Although circumstantial, our results regarding body-mass comparisons of the hatchlings of *Ophiacodon retroversus* suggest that the reproductive mode of this early synapsid might have been somewhat more similar to non-avian reptiles than to other extant amniotes.

The finding of an embryo in an *in ovo* position is a strong support to the hypothesis that the dicynodont *Lystrosaurus* produced eggs (Benoit et al., 2026). Nevertheless, comparisons with extant amniotes as performed herein depict *Lystrosaurus* in the limit between the data fields of non-avian reptiles, birds, and placentals; hence, our analyses are inconclusive regarding to which extant amniote clade the reproductive mode of *Lystrosaurus* was most similar to. A possibility might be that *Lystrosaurus* presented a reproductive strategy in which the egg was retained inside the mother (i.e., extended embryo retention strategy), which could explain the relatively large hatchling size (see Jiang et al., 2023).

The large size of *Lystrosaurus* perinates suggests that this taxon produced small clutches of relatively large individuals. This interpretation contrasts with the reproductive biology comparable to non-avian reptiles proposed for the tritylodontid *Kayentatherium wellesi* (Benoit et al., 2026). The discovery of a large number perinates of *Kayentatherium wellesi* led to the interpretation that at least some early mammaliamorphs retained the purported plesiomorphic condition for amniotes, consisting of a large litter of very small new-born whereas small litters are considered to constitute a derived mammalian trait (Hoffman and Rowe, 2018). Nevertheless, clutch/litter size and mass are dependent on several factors, extrinsic and intrinsic to organisms, and it might be that clutch/litter mass is a more appropriate proxy for inferring the reproductive strategy than clutch/litter size (e.g., Sikes and Ylönen,

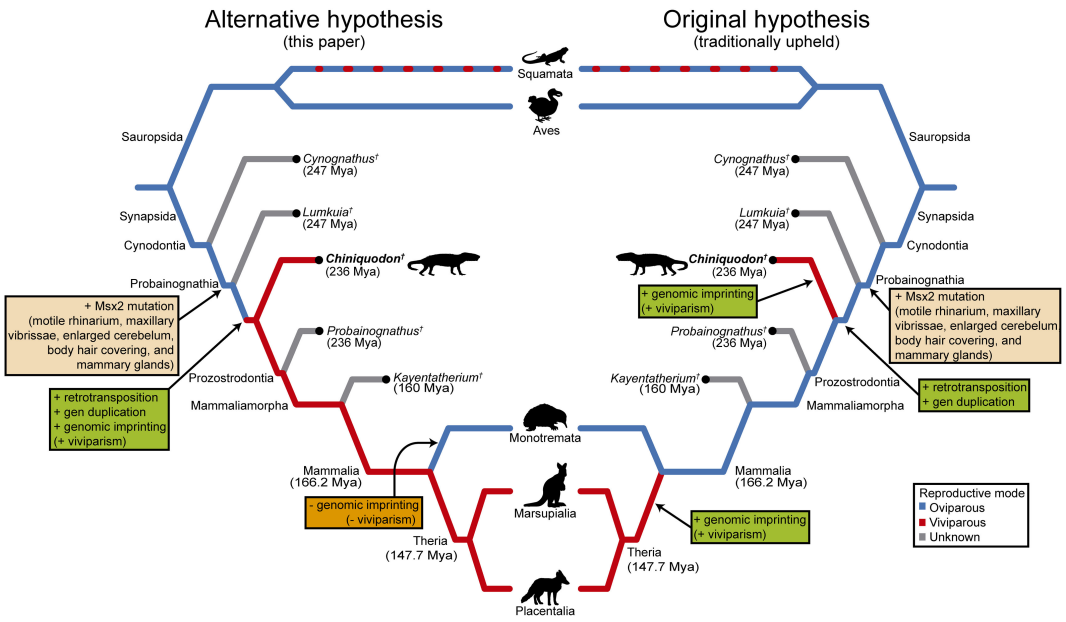

FIGURE 3
Simplified cladograms showing the two equally parsimonious, alternative scenarios for the evolution of viviparity and other features as discussed herein. On the right, the traditional upheld hypothesis, which proposes that oviparity is the ancestral condition for Mammalia and implies the independent origin of viviparity in *Chiniquodon theotonicus* and crown-therians. On the left, the alternative hypothesis, which suggests that viviparity had a single origin in early probainognathians whereas the condition observed in extant monotremes represents a reversal to the ancestral condition. Cladogram topology adapted from Benoit et al. (2022). Age of selected taxa and nodes after Bininda-Emonds et al. (2007) and Gaetano et al. (2022). Mapping and optimization of characters were performed following the usual methodology as described in de Pinna (1991).

1998; Meiri et al., 2020 and references therein). The clutch/litter mass relative to the adult mass inferred for *Kayentatherium wellesi* is not identical or particularly close to that of any extant amniote (Hoffman and Rowe, 2018: figure 3B). The clutch/litter mass of *Kayentatherium wellesi* is lower than expected for any extant mammal or reptile with a similar adult mass but, among relatively large animals, only some placentals (in particular the giant panda *Ailuropoda melanoleuca*) are shown to give birth to litters of so relatively low mass as that inferred for *Kayentatherium wellesi* (Hoffman and Rowe, 2018: figure 3B). Although not included in the originally published dataset, it is interesting to note that *Macropus giganteus* (i.e., the giant kangaroo, one of the largest extant marsupials) has an adult female mass of 41.5 kg and a litter mass of 0.87 g (Supplementary Data S1). Hence, the minimum litter mass hypothesized for *Kayentatherium wellesi* (i.e., 178.6 g) is much higher than expected if it had a marsupial-like reproductive strategy. The analyses performed herein do not allow to discern which group of extant amniotes *Kayentatherium wellesi* is most comparable to. Presently, the reproductive mode of *Kayentatherium wellesi* cannot be determined using the available information. This early mammaliamorph might have presented a different, still unknown reproductive strategy.

Considering the observations above, it might be tempting to suggest that early synapsids (represented by *Ophiacodon retroversus*) had a reptilian-like reproductive strategy (i.e., they were oviparous); dicynodonts (represented by *Lystrosaurus*) had a reproductive strategy that involved extended embryo retention; early probainognathians (represented by *Chiniquodon theotonicus*) had a placental-like reproductive strategy; and *Kayentatherium wellesi* had a reproductive strategy that might have been comparable to those presented by present day monotremes or marsupials. However, it must be acknowledged that this is a highly-speculative evolutionary scenario, in which our analyses are not conclusive regarding the reproductive strategies of *Ophiacodon retroversus*, *Lystrosaurus*, and *Kayentatherium wellesi*.

It has been inferred that multituberculates (as represented by *Kryptobaatar*) were viviparous considering the anatomy of the pelvis and that they acquired this reproductive strategy independently from therian mammals (Kielan-Jaworowska, 1979). Additionally, on the basis of measurements and reconstruction of the purported birth canal, multituberculates were hypothesized to give birth to very small offsprings with relatively narrow skulls when compared to the adults, narrower than in some present-day placentals such as mice but similar to the ratio found in the marsupial *Antechinus stuarti* (Kielan-Jaworowska, 1979). In opposition, Kielan-Jaworowska (1979) argued that if multituberculate laid eggs, these eggs would have been extremely small when compared to the adult size (i.e., smaller than in any known cleidoic egg). It is not presently known how marsupial and placental reproductive strategies evolved. Although it has been suggested that viviparity is a synapomorphy of Theria (Angelini and Ghiara, 1984; Guillette and Hotton, 1986; Lillegraven et al., 1987; Tyndale-Biscoe and Renfree, 1987; Packard et al., 1989), there are those who argued that this condition might have been acquired independently in marsupials and placentals (Sharman, 1970, 1976; Packard et al., 1977). Viviparity in mammals has been proposed to be strongly correlated with an epigenetic process known as parent-of-origin gene expression (i.e., genomic imprinting), which is only recognized in therians (Kaneko-Ishino and Ishino, 2019). Many of the most notable mammalian characteristics (e.g., homeothermy, large brain

size, invasive placentation, nutrient transfer between fetus and female, milk production, maternal behavior associated with milk suckling) have been linked to the development of this mechanism (Keverne, 2014; Renfree et al., 2013). Available evidence from extant mammals suggests that the evolution of genomic imprinting was gradual (Renfree et al., 2009; Kaneko-Ishino and Ishino, 2019). Monotremes lack imprinted regions but the insertion of retrotransposons and the accumulation of repeated elements within their genome have been interpreted as key mechanisms for the subsequent evolution of genomic imprinting (Renfree et al., 2009, 2013). Genomic imprinting is inferred to have been present in the common ancestor of Theria, but it has continued to evolve independently in metatherians and eutherians, becoming more complex in the latter (Guillette and Hotton, 1986; Renfree et al., 2009; Keverne, 2014; Renfree et al., 2013). In marsupials, only six imprinted genes have been identified in the placenta (Renfree et al., 2009, 2013; Keverne, 2014) whereas, in placentals, 55 imprinted genes have been found to be expressed in the longer-lived choriovitelline placenta (Tunster et al., 2013; Keverne, 2014; Kaneko-Ishino and Ishino, 2019). Presently, the implications of genomic imprinting on reproductive biology are not completely understood. In addition, the mechanisms governing the genes involved in genomic imprinting or how genomic imprinting evolved in the marsupial and placental clades are also unclear. Consequently, it is not possible to evaluate how feasible it is for marsupial or placental reproductive strategies to evolve more than once.

If *Chiniquodon theotonicus* was viviparous, as our results suggest, this invites a revisiting of the evolutionary history of this reproductive mode among synapsids. The mapping of viviparity and oviparity on a phylogenetic reconstruction results in two equally parsimonious scenarios (Figure 3). One of them, representing the traditional view, hypothesizes that oviparity is the ancestral condition for crown Mammalia (Renfree et al., 2009; Ferner et al., 2017). According to this, the viviparous reproductive mode proposed for *Chiniquodon theotonicus* represents an independent, non-homologous event of acquisition of viviparity from therians, with genomic imprinting evolving independently at least twice in the clade (i.e., in *Chiniquodon theotonicus* and in Theria). Retrotransposition and gene duplication are best interpreted as having happened once among synapsids (i.e., in the clade reuniting *Chiniquodon theotonicus* and crown-mammals or earlier). This supports the idea that the genetic basis for viviparity, retrotransposition and gene duplication on the one hand and genomic imprinting on the other, evolved in a step-way manner (Renfree et al., 2009; Kaneko-Ishino and Ishino, 2019). Under this view, viviparity in *Chiniquodon theotonicus* represents yet another case of independent origin of this reproductive mode among vertebrates (Blackburn, 1999, 2015). In the alternative scenario, a single, homologous event of acquisition of viviparity among synapsids is hypothesized. This reproductive mode was achieved early in the mammalian lineage, whereas a reversion to the ancestral oviparous condition is displayed by monotremes. Viviparity is thus interpreted to be plesiomorphic for crown Mammalia. The evolutionary history of retrotransposition, gene duplication, and genomic imprinting is suggested to be coupled. Hence, the genetic basis for viviparity is best interpreted to have originated in a single event among Triassic probainognathians, at least in the clade defined by *Chiniquodon theotonicus* plus mammals. Being equally parsimonious, it cannot be determined which hypothesis is more likely. However, it should be noted that the first one favors instances of homoplasy (i.e., multiple acquisitions of viviparity) whereas the second one upholds the homology of viviparity while requiring a reversal to the ancestral condition in monotremes (Figure 3) (de Pinna, 1991).

4 Materials and methods

4.1 Specimen studied

Specimen CRILAR-PV109 was buried in light olive grey and light bluish grey tuffaceous siltstones deposited in a littoral low-energy mudflat (Mancuso et al., 2020). The specimen is well preserved and includes: the skull, vertebrae (i.e., both atlas arches, axis, and cervical, dorsal, and caudal vertebrae), ribs, elements of the pectoral and pelvic girdles (i.e., clavicle, scapula, ilium, ischium, and pubis), limb bones (i.e., radius, ulna, radial, carpals, metacarpals, femur, tibia, fibula tarsals, metatarsals, and phalanges). More than 50% of the skeleton of CRILAR-PV109 is partially articulated, exhibiting an equal representation of the anterior and posterior portions of the animal. The remains occupy a superficial area of approximately 0.12 m^2 within a single stratigraphic horizon. The partially disarticulated elements are still associated with a slightly random dispersal pattern, most probably related to the action of low-energy currents as suggested by the Voorhies group analysis (Mancuso et al., 2014). Furthermore, the bones exhibit post-mortem modifications, such as uniform, slight cracking and flaking, consistent with weathering stage 0-1 (sensu Behrensmeyer, 1978). This suggests a brief period of subaerial exposure prior to burial and an absence of time-averaging for the assemblage. The taphonomic features observed, the consistent size of the bones, and the absence of duplicated elements support that they represent a single individual.

The specimen CRILAR-PV109 was positively assigned to *Chiniquodon theotonicus* on the basis of the presence of the following combination of diagnostic characters of this species (Abdala and Giannini, 2002): secondary well-developed palate, relatively short snout, angulation (c. 110° or more) between the ventral edge of the maxillary zygomatic process and the anteroventral margin of the jugal, greatly elongated pterygoid flanges ending in a thin projection and directed posteroventrally, and sectorial postcanine teeth having no cingula and with their main cusp lacking serrated edges.

4.2 Institutional abbreviations

CRILAR-PV, Centro Regional de Investigaciones Científicas y Transferencia Tecnológica de La Rioja, Argentina; MCZ, Museum of Comparative Zoology, Harvard University, U.S.A.; PVL, Paleontología Vertebrados Lillo, Instituto Miguel Lillo, Argentina.

4.3 Histological methodology

In order to analyze the bone microstructure of *Chiniquodon theotonicus* specimen CRILAR-PV109, thin sections from the right ulna and the left femur were performed. The transverse sections were obtained from the midshaft of each element. To avoid loss of anatomical information, a cast of the sectioned elements was made before sampling. The thin sections were prepared at Paleohistological Laboratory of the Museo Provincial Carlos Ameghino (Cipolletti, Argentina), using the standard methods outlined by Cerda et al. (2020), and analyzed using a petrographic polarizing microscope (Leica DM750P). The nomenclature and definitions of structures used in this study are derived from Francillon-Vieillot et al. (1990) and de Buffrénil and Quilhac (2021).

4.4 Mass estimations

Anyonge (1993) proposed mass-estimation equations based on the femoral circumference measurements in modern carnivores. To produce these equations, he employed least-squares regressions of $\log_{10}$ transformed data. The relationship between the dependent and independent variables (body mass and femoral circumference at midshaft, respectively) is expressed as the power function:

$$\log_{10}(\text{body mass in kg}) = k.\ \log_{10}(\text{femoral circumference in mm}) + \log_{10}(b)$$

Where the slope, k, and the intercept, $log_{10}(b)$, vary according to the mammal group in which the equation is based.

The equation produced using data from all considered carnivoran species is:

$$\log_{10}(\text{body mass in kg}) = 2.88.\ \log_{10}(\text{femoral circumference in mm}) - 3.4$$

That produced using felid species measurements is:

$$\log_{10}(\text{body mass in kg}) = 2.92.\ \log_{10}(\text{femoral circumference in mm}) - 3.46$$

The one that resulted from analyzing canids is:

$$\log_{10}(\text{body mass in kg}) = 2.37.\ \log_{10}(\text{femoral circumference in mm}) - 2.6$$

The body mass of *Chiniquodon theotonicus* (CRILAR-PV109) was calculated using these three models. We estimated its weight at the time of birth and death from the femoral circumference at midshaft, measuring the neonatal line (17.3 mm) and the external surface (35.81 mm), respectively.

The body mass at the time of birth and death of *Ophiacodon retroversus* was also estimated using the above models but considering the humeral circumference instead of the femoral one. For this purpose, we used the circumference represented by the hatchling line (preserved in specimen MCZ-5926 - MOS II; 20.828 mm) and the external surface represented by the external fundamental system (preserved in specimen MCZ-1486 - MOS V; 44 mm).

For these measurements, we employed the software ImageJ 1.45s (Schneider et al., 2012).

The equation based on data from extant carnivorans (van Valkenburgh, 1990; Mancuso et al., 2014) that links body mass and skull length (measured from the anterior tip of the snout to the posterior end of the occipital condyles) was employed to test our results (i.e., calculate the body mass of *Chiniquodon theotonicus* specimen CRILAR-PV109 at the time of death and its predicted skull length at the time of birth):

$\log_{10}(\text{body mass in kg}) = 3.13.\ \log_{10}(\text{skull length in mm}) - 5.59$

4.5 Discriminant analysis and K-nearest neighbors test

We performed a discriminant analysis and a K-nearest neighbors test as implemented in the software Past 4.16c (Hammer et al., 2001). The variables employed were the decimal logarithm of the body masses enumerated in Supplementary Data S1–S3, the body masses estimated for *Ophiacodon retroversus*, *Lystrosaurus*, and *Kayentatherium wellesi*, and the average of the weight estimates from *Chiniquodon theotonicus* specimen CRILAR-PV109 (Supplementary Data S4). For the K-nearest neighbors test, extant amniotes represented the training set whereas extinct taxa were to be alternatively classified. We employed the weighting scheme due to Gou et al. (2012), Euclidean and Manhattan distance indexes were considered, and the parameter K was varied from 1 to 1400.

Data availability statement

The original contributions presented in the study are included in the article/Supplementary Material. Further inquiries can be directed to the corresponding author.

Ethics statement

The manuscript presents research on animals that do not require ethical approval for their study.

Author contributions

LG: Writing – review & editing, Funding acquisition, Visualization, Formal analysis, Writing – original draft, Conceptualization, Methodology, Investigation. MB: Writing – review & editing, Visualization. IC: Methodology, Conceptualization, Investigation, Visualization, Formal analysis, Writing – review & editing, Writing – original draft. AM: Funding acquisition, Writing – review & editing.

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Conflict of interest

The author(s) declared that this work was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmamm.2026.1845319/full#supplementary-material

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